SYSTEMATICS AND BIOLOGY OF A NEW, POLYPHAGOUS SPECIES OF *MARMARA* (LEPIDOPTERA: GRACILLARIIDAE) INFESTING GRAPEFRUIT IN THE SOUTHWESTERN UNITED STATES

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Abstract.—A new species of *Marmara* (Lepidoptera: Gracillariidae), **M. gulosa Guillén and Davis**, from the southwestern United States, is described and illustrated. This species, the citrus peelminer, which was previously misidentified as *M. salictella* Clemens, is a cyclical pest in xeric areas of California and Arizona. Larvae mine the surface of citrus fruits, with grapefruit, *Citrus paradisi* Macfadyen, as a preferred host, and with oleander, *Nerium oleander* L., cotton, *Gossypium hirsutum* L., and avocado, *Persea americana* Mill., as alternate hosts. *Salix lasiolepis* Benth is probably the primary host. Based on two nuclear gene regions, 28S-D2 and ITS2, almost no genetic differences were found between populations of peelminer on oleander and grapefruit (0–0.4%), whereas both populations had a 6.8–9.2% divergence from an undescribed, sympatric species of *Marmara* on tree tobacco. Thus at the morphological and genetic level the populations on oleander and grapefruit appear to be panmictic. On grapefruit in the laboratory, females laid 48.5 ± 7.2 eggs and developmental time (egg-adult) at 26°C was 28.8 ± 0.4 days.

Key Words: citrus, cotton, avocado, oleander, willow, *Marmara*, peelminer, biology, hypermetamorphosis, morphology, 28S-D2, ITS2

The citrus peelminer has been reported mining the peel of citrus fruits in the southwestern United States since the early part of the twentieth century (Vinal 1917; Essig 1926; Lockwood 1933; Quayle 1938; Woglum 1948; Anonymous 1960; Atkins 1961, 1971; Chong and La Rosa 1986; Reeves 1995; Gibson et al. 1997). The earliest known collection of this insect consists of a mined orange (*Citrus sinensis* Osbeck) peel collected 23 July 1915 at Pasadena, California (USNM). It has been reported as an economic pest in California (Atkins 1961, 1971; Reeves 1995), Arizona (Anonymous 1960, Gibson et al. 1997) and Cuba (Chong and La Rosa 1986). It also reputedly occurs in very low numbers in Texas and Florida (H. Browning, Manners, in litt.), although no adults from citrus collected outside of California have been examined. Citrus fruit mines from Texas and Florida could also be the result of the citrus leafminer, *Phyllocnistis citrella* Stainton (Gracillariidae), which has become well established along the southern United States and through much of the Neotropical citrus growing regions after 1993, and now in California (Heppner 1993, 1995; Heppner and Dixon 1995; Hoy and Nguyen 1997; JMH unpublished). Larvae of the citrus peelminer form long serpentine mines (Fig. 1) that disfigure the epidermal surface of the fruit (Atkins 1961), and under heavy infestations, the entire fruit surface may be-
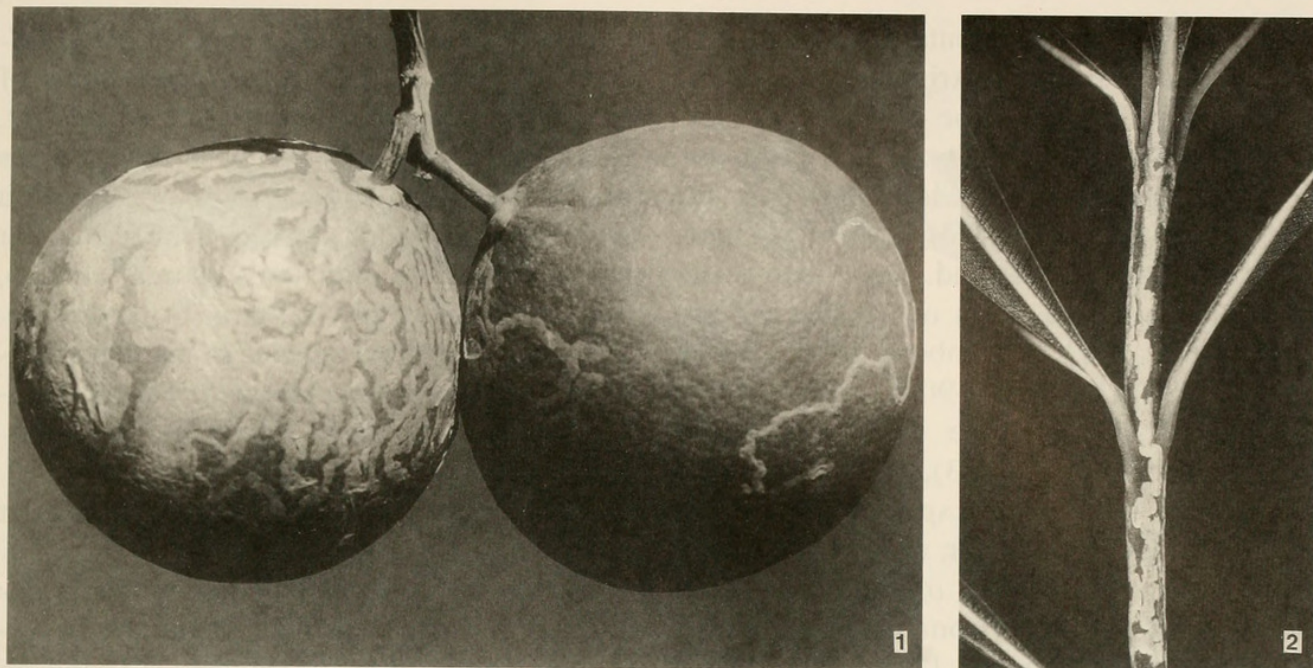
Figs. 1–2. *Marmara gulosa,* larval mines. 1, On grapefruit, *Citrus paradisi.* 2, On oleander, *Nerium oleander* (photo courtesy of E. L. Reeves).

come blistered (Reeves 1995). The damage is cosmetic because the internal quality of the fruit is not affected, however the fruit is rendered unacceptable for the fresh fruit market (Atkins 1961, Reeves 1995).

Citrus peelminer was first identified as a western form of *Marmara salictella* Clemens (Lepidoptera: Gracillariidae), a miner on young twigs of willow in the Atlantic states (Woglum 1948), and since, has been reported as this species (Lockwood 1933, Woglum 1948, Anonymous 1960, Atkins 1961, Chong and La Rosa 1986, Reeves 1995, Gibson et al. 1997). Although morphologically closely allied to *M. salictella,* citrus peelminer adults reared from citrus fruit from the Coachella Valley, California, represent a distinct, previously undescribed species.

Besides *Citrus* (Rutaceae), other plants previously reported as hosts for the citrus peelminer include willow (*Salix* sp.) in California (Woglum 1948, Atkins 1971); oleander (*Nerium oleander* L.) in California (Atkins 1961, Reeves 1995) and Arizona (Gibson et al. 1997); watermelon (*Citrullus vulgaris* Schrad.) in California (Atkins 1971); cotton (*Gossypium hirsutum* L.) in

Arizona (Atkins 1971); mesquite (*Prosopis* sp.) and grape (*Vitis vinifera* L.) in Arizona (Gibson et al. 1997). On citrus, citrus peelminer mines the peel of fruits, with grapefruit as a preferred host, although tangerines, oranges, lemons and limes are also mined (Atkins 1961, 1971, Gibson et al. 1997). Less frequently, larvae mine the green shoots of lemon, tangerine (Atkins 1971, Gibson et al. 1997), grapefruit and tangelo cultivar Minneola (Gibson et al. 1997). On oleander (Fig. 2), shoots and leaves are mined (Atkins 1961, Reeves 1995, Kerns, in litt.); on watermelon, fruits are mined (Atkins 1971), and on mesquite, grape and cotton, stems are mined (Gibson et al. 1997, D. Kerns, personal communication). All of the above host plants have been previously considered as alternate hosts for the citrus peelminer because they grow in close proximity to peelminer-infested citrus.

Information on alternate host plants for the citrus peelminer is essential to identify sources of citrus infestation of this pest. Oleander plants are abundant in the Coachella Valley, being present as hedges surrounding groves or houses, serving as

windbreaks, as ornamental planting or as individual plants. In Arizona, cotton and citrus are grown in close proximity in several areas where oleander is also abundant.

The genus *Marmara* is endemic to the New World. Including *M. gulosa,* 22 species have been described. Seventeen occur in North America north of Mexico (Clemens 1860, 1863; Chambers 1875; Busck 1906, 1909; Braun 1909; Vinal 1917; Forbes 1923; DeGryse 1943; Fitzgerald 1973, 1975; Davis 1983), with at least 12 additional, undescribed species known (D. R. Davis and D. Wagner, unpublished). Six species (including *M. opuntiella* Busck) have been reported from South America (Bondar 1939; Meyrick 1915, 1918; Davis 1984). Recent fieldwork in Costa Rica by Wagner and Davis (unpublished) has revealed the presence of a rich Neotropical gracillariid fauna from the La Selva Biological Reserve, Costa Rica. *Marmara* from this area are especially prevalent on the monocot families Araceae and Heliconiaceae. Alibert (1951) mistakenly reported one species from Africa, but his illustration of the adult and, more importantly, his description of the last instar larva "cinq paires de fausses pattes" indicates another, more atypical, possibly oecophyllembiine genus with four pairs of abdominal prolegs.

Of the North American species of *Marmara,* two occur in Canada (British Columbia) (Clemens 1860, Fitzgerald 1975) and eleven in the northern United States (Clemens 1860, 1863; Chambers 1875; Braun 1909; Busck 1909; Vinal 1917; Forbes 1923; Fitzgerald 1973, 1975). Only two of the described species occur in southern areas, *M. guilandinella* Busck (Vinal 1917) from Florida and *M. opuntiella* (Busck 1906) from southern Texas, ranging also into the northern neotropics (Mann 1969). In southern California, unidentified species of *Marmara* have been found on different host plants in five different families: leaves of *Umbellularia californica* Nutt. (Umbelliferae), stems of *Rhamnus californica* Esch. (Rhamnaceae), stems of *Prunus ili-*

cifolia D. Dietr. and *Heteromeles arbutifoliella* M. Roemer (Rosaceae), and stems of *Acer macrophyllum* Pursh (Aceraceae) (D. Frack, in litt.). Another undescribed species of *Marmara* is sympatric in distribution with *M. gulosa* in southern California but mines the leaves and stems of tree tobacco, *Nicotiana glauca* Graham (Solanaceae). The only described species in southern California is *Marmara arbutiella* Busck, mining *Arbutus menziesii* Pursh and *Arctostaphyllos andersonii* A. Gray (Wagner et al. 2000), neither of which occur in the desert region of California.

In this study, the citrus peelminer is described and alternate host plants are investigated. We focused on *Marmara* found on citrus and oleander, although miners discovered on avocado, cotton, and willow were also investigated. Specimens from these host plants were collected and compared with the citrus peelminer by utilizing external morphology of adults and, where possible, immature stages. As a means for testing conclusions derived from morphological studies, genetic comparisons of two nuclear genes from moths reared from grapefruit, oleander, and tree tobacco were also examined.

Marmara gulosa Guillén and Davis, new species
(Figs. 1–3, 5–10, 11–47)

Adult (Fig. 3).—Forewing length: 2.3–2.6 mm.

Head: Vestiture smooth, scales curving down over frons; scales on vertex mostly silvery gray with brown tips; frons mostly silvery white with brown-tipped scales adjacent to mouthparts; a broad band of grayish brown scales across back of head. Antenna about 0.8 × length of forewing; flagellum with a single annulus of slender, usually brown scales; scape brown dorsally, cream ventrally. Ocellus absent. Length of maxillary palpus about half vertical diameter of eye; cream dorsally, dark brown ventrally and laterally and with brown distal end. Haustellum elongate, about 2.0 ×
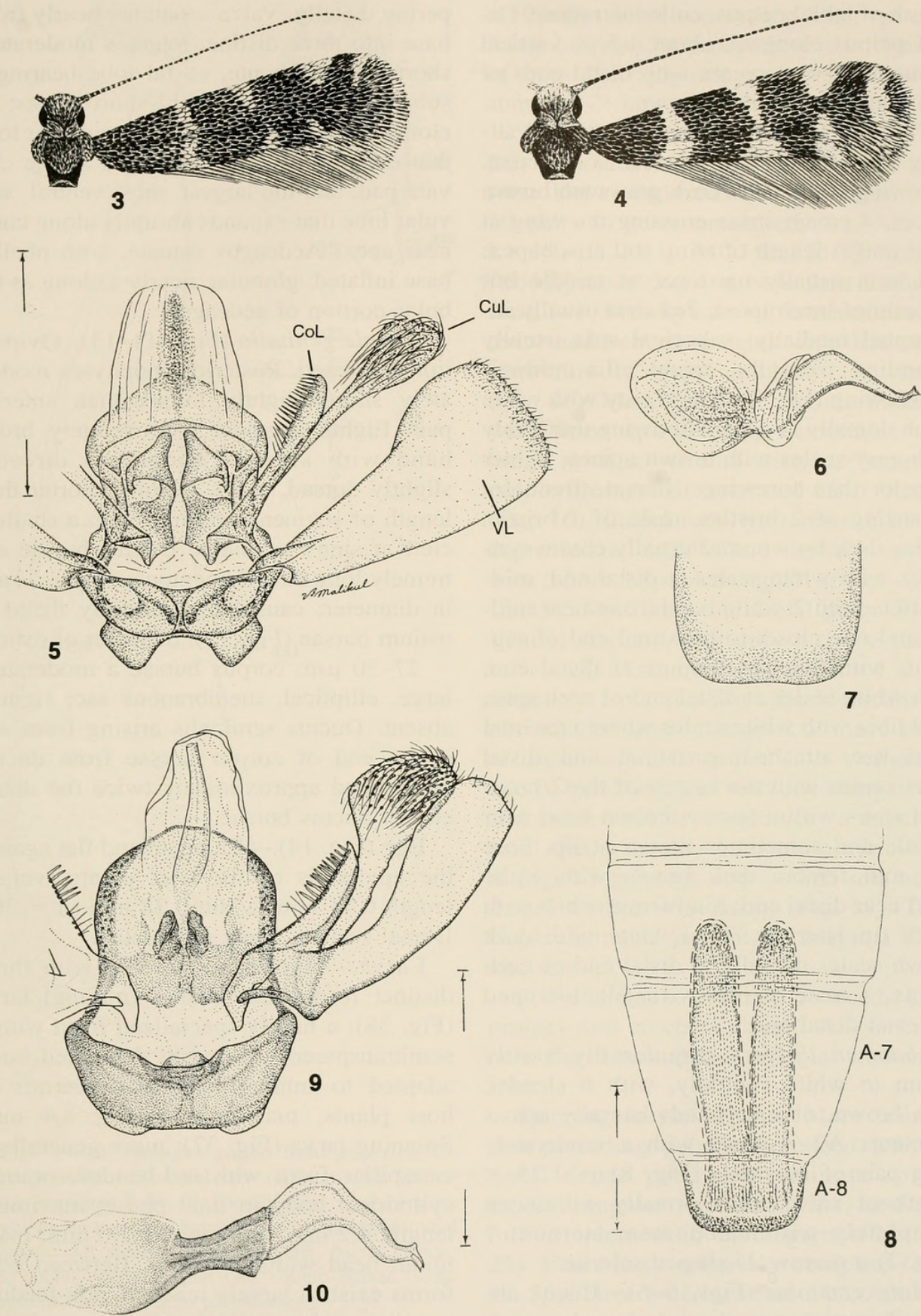
Figs. 3–10. *Marmara* adults. 3, *M. gulosa* from grapefruit, (2.4 mm). 4, *M. salictella*, from *Salix* sp. (2.7 mm). Length of forewing in parentheses. 5–10, Male genitalia and abdominal morphology. 5, *M. gulosa* from grapefruit, ventral view, (0.25 mm; CoL = costal lobe, CuL = cucullar lobe, VL = valvular lobe). 6, Aedeagus, lateral view. 7, Eighth sternum. 8, Coremata inside abdominal segments A6–8, (0.5 mm). 9, *M. salictella*, ventral view, (0.25 mm). 10, Aedeagus, lateral view. (Scale lengths in parentheses.)

length of labial palpus, coiled in repose. Labial palpus elongate, about 1.5 × vertical diameter of eye, cream with distal ends of 2nd and 3rd segments brown.

Thorax: Dorsum with brown-tipped silvery gray scales; venter cream over coxa. Forewing with scales dark gray with brown apices, 4 cream striae crossing the wing at ¼, ½ and ¾ length of wing and at subapex; 2nd stria usually narrower at middle but sometimes interrupted; 3rd stria usually interrupted medially; subapical stria usually extending from the apical cilia midway across wing (Fig. 3); fringe gray with white patch dorsally at apex. Hindwing uniformly with gray scales with brown apices, lighter in color than forewings. Female frenulum consisting of 2 bristles, male of 1 bristle. Tibiae dark brown, and usually cream ventrally, with white scales at distal end; middle tibia with 2 white bands, one near middle and one closer to proximal end of segment; with two black spurs at distal end, with white scales at distal end of each spur; hind tibia with white scales where proximal spurs are attached; proximal and distal spurs cream with the largest of the 2 proximal spurs with a narrow brown band near middle and sometimes brown at tip. Fore and mid femora dark brown with white band near distal end; hind femur white with black tip laterally. Tarsi white with dark brown scales dorsally at distal end of each tarsus. Coxae white with black-tipped scales at distal end.

Abdomen: Silvery gray dorsally, mostly cream to white ventrally, with 6 slender, dark brown, oblique bands laterally across segments A2–7. Male with a moderately long pair of coremata (Fig. 8) ~ 1.25 × length of valva, and normally withdrawn completely within abdomen; sternum 7 (Fig. 7) a narrow, U-shaped sclerite.

Male genitalia (Figs. 5–6): Uncus absent. Tegumen a moderately broad, rounded, dorsal band. Vinculum a moderately broad, ventral band with a pair of small round lobes protruding from anterior margin. Gnathal arms separate, stout, and ta-

pering distally. Valva separated nearly from base into three distinct lobes: a moderately short, slender, acute, costal lobe bearing a subapical row of ~ 10–12 short spines; an elongate, slender, more lateral, cucullar lobe that expands distally to form a setose clavate pad, and the largest, most ventral, valvular lobe that expands abruptly along costa near apex. Aedeagus sinuate, with phallobase inflated, globular, nearly as long as tubular portion of aedeagus.

Female genitalia (Figs. 11–13): Ovipositor shortened. Posterior apophyses moderately short, slightly longer than anterior pair. Eighth segment a moderately broad band with anterior apophyses directed slightly dorsad, short, slightly shorter than length of segment; sternum with a shallow cleft at sinus vaginalis. Ductus bursae extremely long and filamentous, only ~ 11 μm in diameter; caudal end abruptly flared at ostium bursae (Fig. 13); diameter of ostium ~ 27–30 μm; corpus bursae a moderately large, elliptical, membranous sac; signum absent. Ductus seminalis arising from opposite end of corpus bursae from ductus bursae and approximately twice the diameter of ductus bursae.

Egg (Fig. 14).—Elongate and flat against the epidermis of the host plant; average length 0.41 mm, width 0.28 mm (n = 30). Dorsal surface finely reticulated.

Larva.—Hypermetamorphic with three distinct forms. Sapfeeding (mining) larva (Fig. 38): a highly specialized form with a semitransparent-yellowish, depressed body adapted to mining beneath epidermis of host plants; maximum length, 4.4 mm. Spinning larva (Fig. 37): more generalized caterpillar form with red-banded, orange, cylindrical body in final phase; maximum length, 4.2 mm; body width, 1.0 mm; maximum head width, 0.4 mm. Between both forms exists a largely inactive, non-feeding transitional form which does not molt but remains within cuticle of last mining instar (DeGryse 1916; Vinal 1917; Fitzgerald and Simeone 1971; Fitzgerald 1973, 1975; Kumata 1978; Davis 1987, 1998; Wagner et
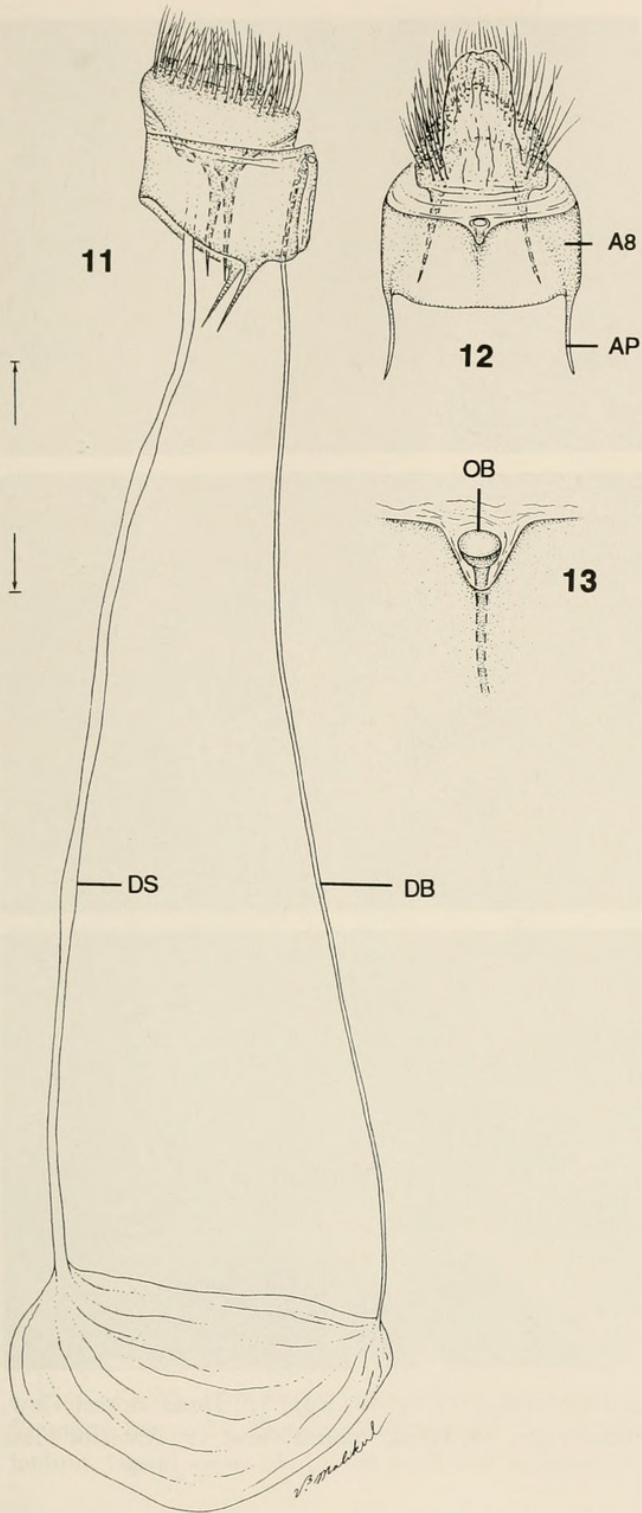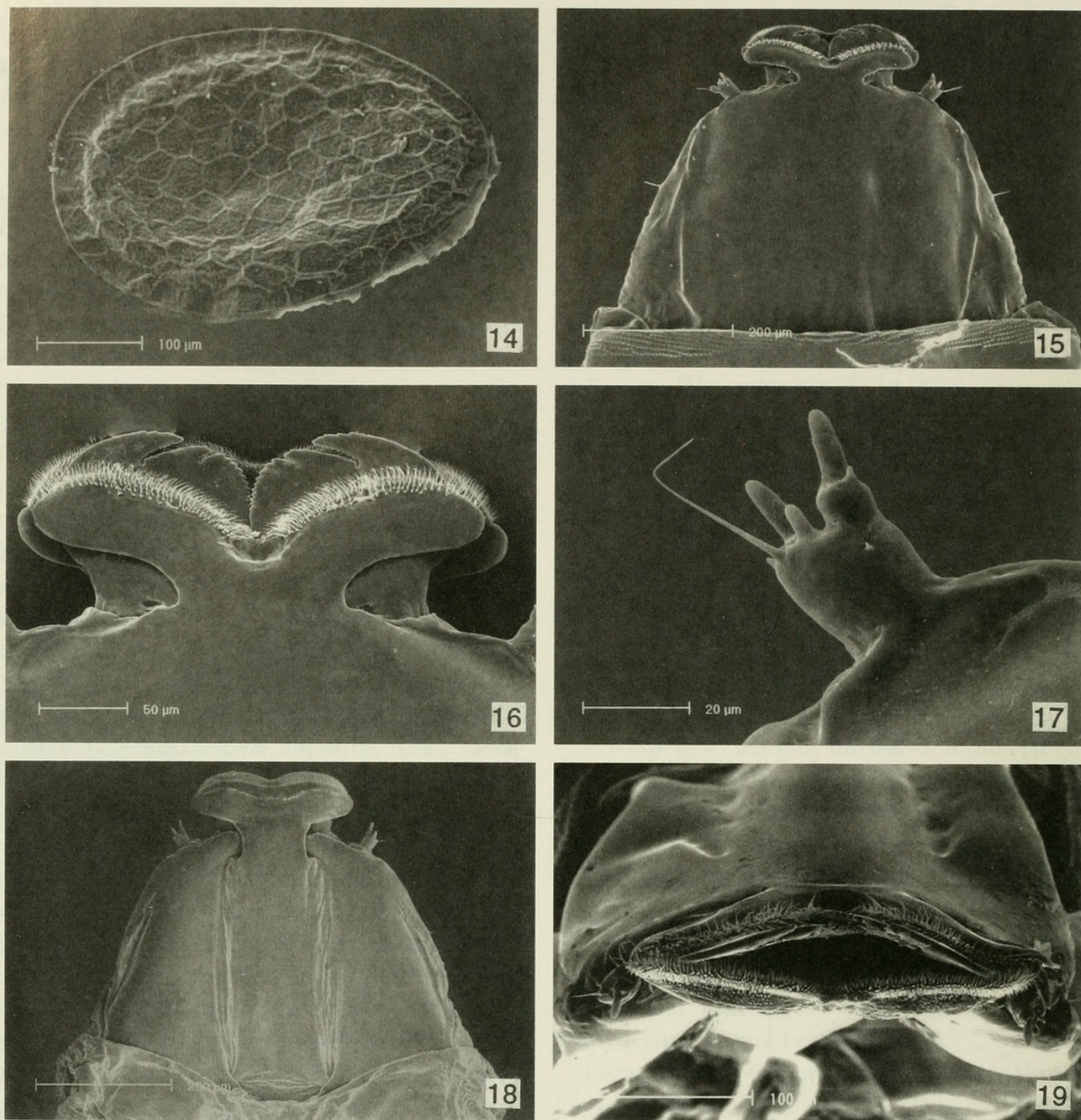
Figs. 11–13. *Marmara gulosa* from grapefruit, female genitalia. 11, Lateral view (0.5 mm). 12, Ventral view, segments 8, 9+10. 13, Enlarged view of sinus vaginalis and ostium bursae. (A8, eighth abdominal segment; AP, anterior apophysis; DB, ductus bursae; DS, ductus spermathecae; OB, ostium bursae. Scale length of Figs. 11–12 in parentheses.)

al. 2000). When succeeding final, spinning instar emerges, it proceeds to shed cuticles of both last spinning and transitional instars.

Sapfeeding larva.—*Head:* Greatly depressed and triangular (Figs. 15, 20). Most setae lost or reduced: dorsal cranium with 10 pairs of setae preserved, A1, A2, A3, L1, P1, P2, MD1, MD2 and MD3. Labrum strongly constricted at base then flaring to form two, broadly curved, lateral lobes; anterior and ventral margins with dense concentration of short epipharyngeal spines (Fig. 16). Mandible large, greatly flattened, with three apical cusps; innermost cusp broad with a serrated margin; outermost cusp with serrated outer and inner margins (Fig. 16). Labial lobe with anterior margin depressed at middle and densely covered with short hypopharyngeal spines (Figs. 18–19). Maxillary and labial palpi absent. Ventral cranium with only a single pair of setae (S2). Antenna two-segmented with a relatively stout sensillum basiconicum and two smaller sensilla on apex of much smaller distal segment (not always well-developed); basal segment with one elongate seta and three sensilla basiconica: a relatively stout one, a smaller one, and a minute one at edge of segment, and a small seta on the dorsal surface of segment (Fig. 17). Three black stemmata present, of irregular shape and size.

Body: Setae extremely reduced. Legs, prolegs and crochets absent. A1–9 banded near the dorsoanterior margin with small spines.

Spinning larva.—*Head:* More rounded than preceding, poorly sclerotized, with distinct, dense patches of minute spines, broadly angular in lateral view, and with full complement of mouthparts (Figs. 21–22). Chaetotaxy relatively complete (Figs. 33–35): three anterior setae (A1, A2, A3), three stemmatal setae (S1, S2, S3), three substemmatal setae (SS1, SS2, SS3), one lateral seta (L1), two posteriodorsal setae (P1, P2) and three dorsal setae (MD1, MD2, MD3) present; frontal and adfrontal

Figs. 14–19. *Marmara gulosa* from grapefruit, egg and sapfeeding larva. 14, Egg. 15, Head, dorsal view. 16, Labrum and mandibles, dorsal view. 17, Antenna, ventral view. 18, Head, ventral view. 19, Anterior view of mouthparts.

setae absent. Six stemmata arranged in a semicircle, with sixth usually greatly reduced, indistinct (Fig. 35). Antenna similar to mining larva but both setae of segment II considerably longer (Fig. 23). Labrum reduced, largely fused to cranium, and notched at center, with three pairs of setae (Figs. 21, 33). Mandible with five cusps, two distal and distinct, and three smaller; with two setae on lateral surface (Fig. 36).

Maxillary palpus well-developed and composed of three distinct segments; proximal segment with three long setae (including dorsal seta of reduced mesal lobe); middle segment with seta at apex; distal segment elongate with two setae, plus one short and two very small setae at apex, and an elongate sensillum digitiformium mid-dorsally; mesal lobe (laciniogalea, in Grimes and Neunzig 1986) indistinct, with single stout,
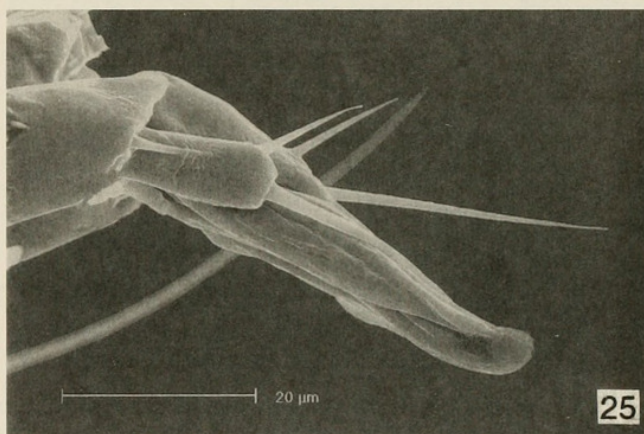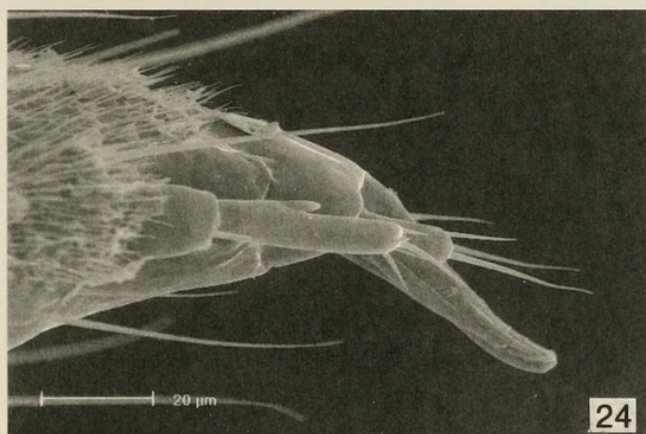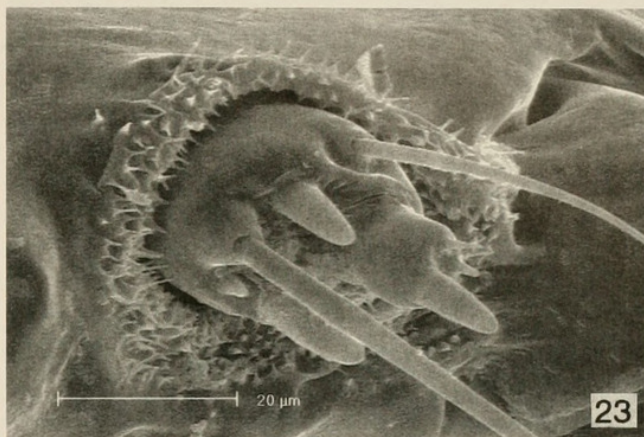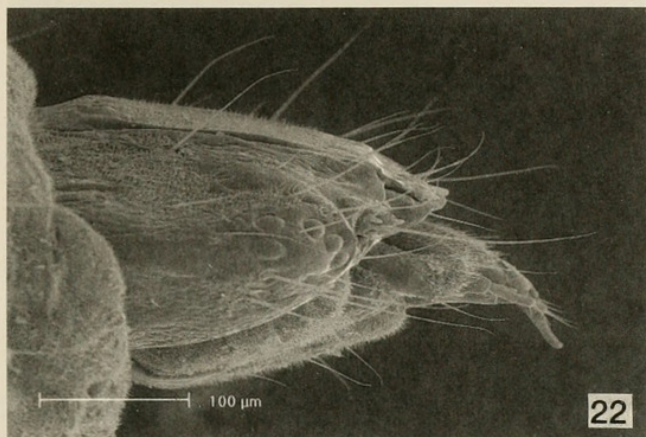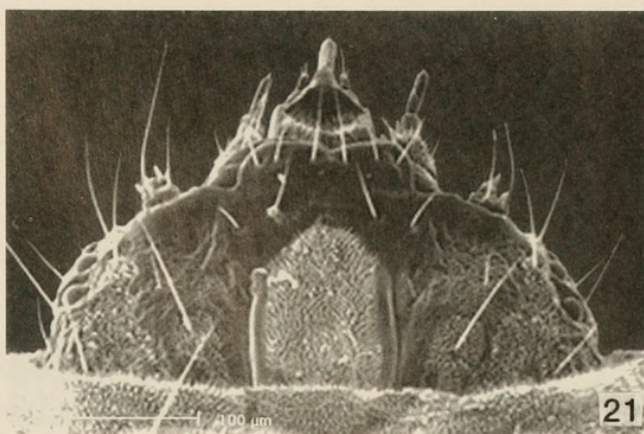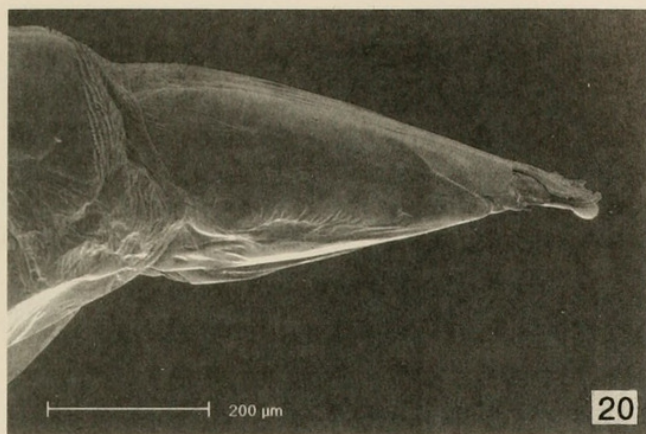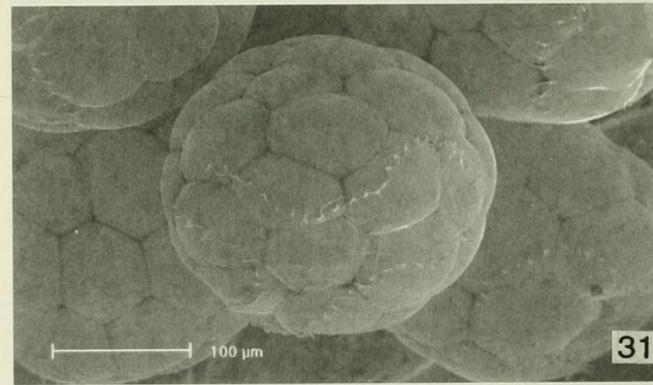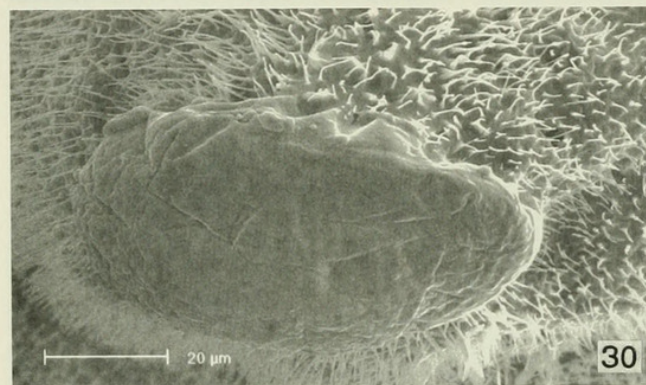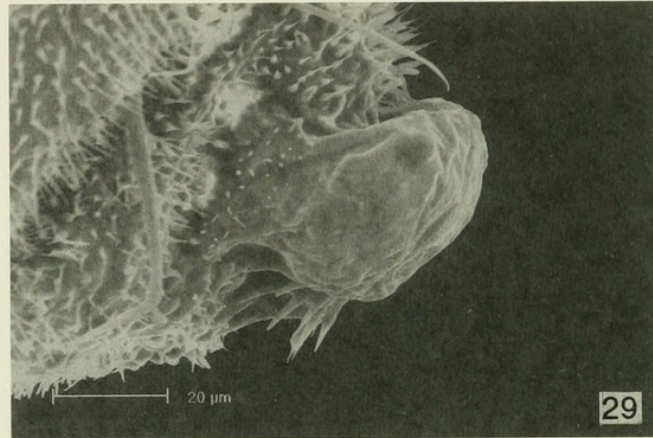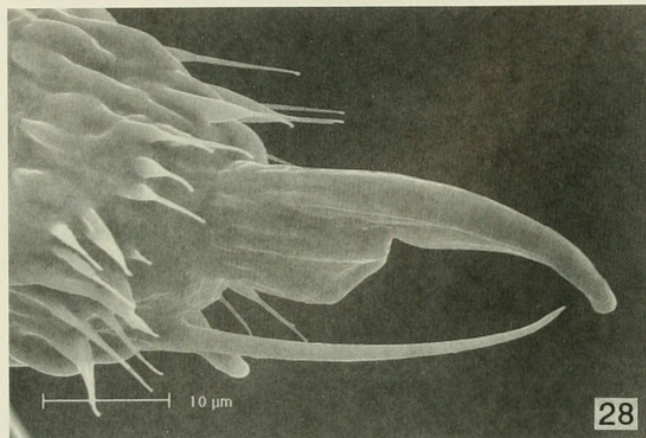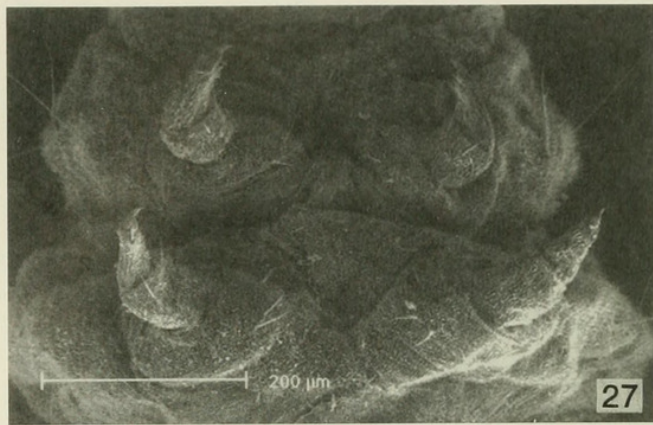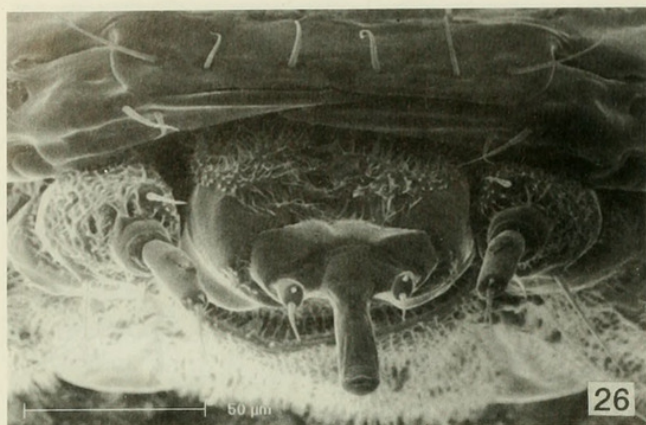
Figs. 20–25. *Marmara gulosa* from grapefruit larva. 20, Sapfeeding larva, lateral view of head. 21–25, Spinning larva, 21, Dorsal view of head. 22, Head, lateral view. 23, Antenna, lateral view. 24, Maxilla and labium, lateral view. 25, Labial palpi and spinneret, lateral view.

dorsal seta (Fig. 24). Labium with prominent spinneret; labial palpus moderately short, two-segmented, with two setae at apex of distal segment and a shorter seta at base (Figs. 25, 34).

Thorax: Setae more conspicuous than in sapfeeding larva. MD1 present on T2–3. D group bisetose on T1–3. XD1 present on T1; XD2 absent. SD bisetose on T1–3. L group bisetose on T1, unisetose on T2–3 (Fig. 32).

Abdomen: MD1 present on A1–9. D group bisetose on A1–9. SD and L group unisetose on A1–9. SV bisetose on A1–8, absent on A9. V group unisetose on A1–7, absent on A8–9 (Fig. 32). Rudimentary prolegs on A3–5 and 10 (Figs. 29, 30); ventral prolegs with anterior row of 4–7 crochets (Fig. 29). Anal plate with dorsal, lateral, subventral and ventral setae; anal prolegs devoid of crochets.

Pupa (Figs. 39–46).—Maximum length:

Figs. 26–31. *Marmara gulosa* from grapefruit, spinning larva and cocoon. 26, Labial palpi and spinneret. 27, Thorax, ventral view. 28, Pretarsus, lateral view. 29, Abdominal proleg, lateral view. 30, Abdominal proleg, ventral view. 31, Cocoon globules.

2.9 mm; width: 0.7 mm. Light brown in color. Vertex with broadly triangular, minutely serrated apical process (cocoon cutter) (Figs. 41–42) which appears ridge-like, viewed laterally. Setae absent from frontal area. Mandible visible as a small sclerite partially covered by the labrum (Fig. 41). Maxilla extend to A4. Sheath for antenna approximately same length or slightly longer than wings and usually extending to A7. Foreleg slightly shorter than maxilla. Midleg usually extends to A5. Hindleg usually

reaching A9–10 (Fig. 39). Chaetotaxy as in Fig. 40; all setae extremely short. Spiracles well developed on A2–8. Anterior fifth of dorsum of A3–7 with dense concentration of small, stout spines mostly arranged into 4–5 scattered rows (Figs. 40, 43); tergal spines more reduced and scattered over A8–9. A10 with three pairs of similar, short, stout, cremasteral spines; one pair dorsally and two pairs laterally (Figs. 44–46).

Cocoon.—Consists of a firm sheet of white silk over some crevice in bark or on
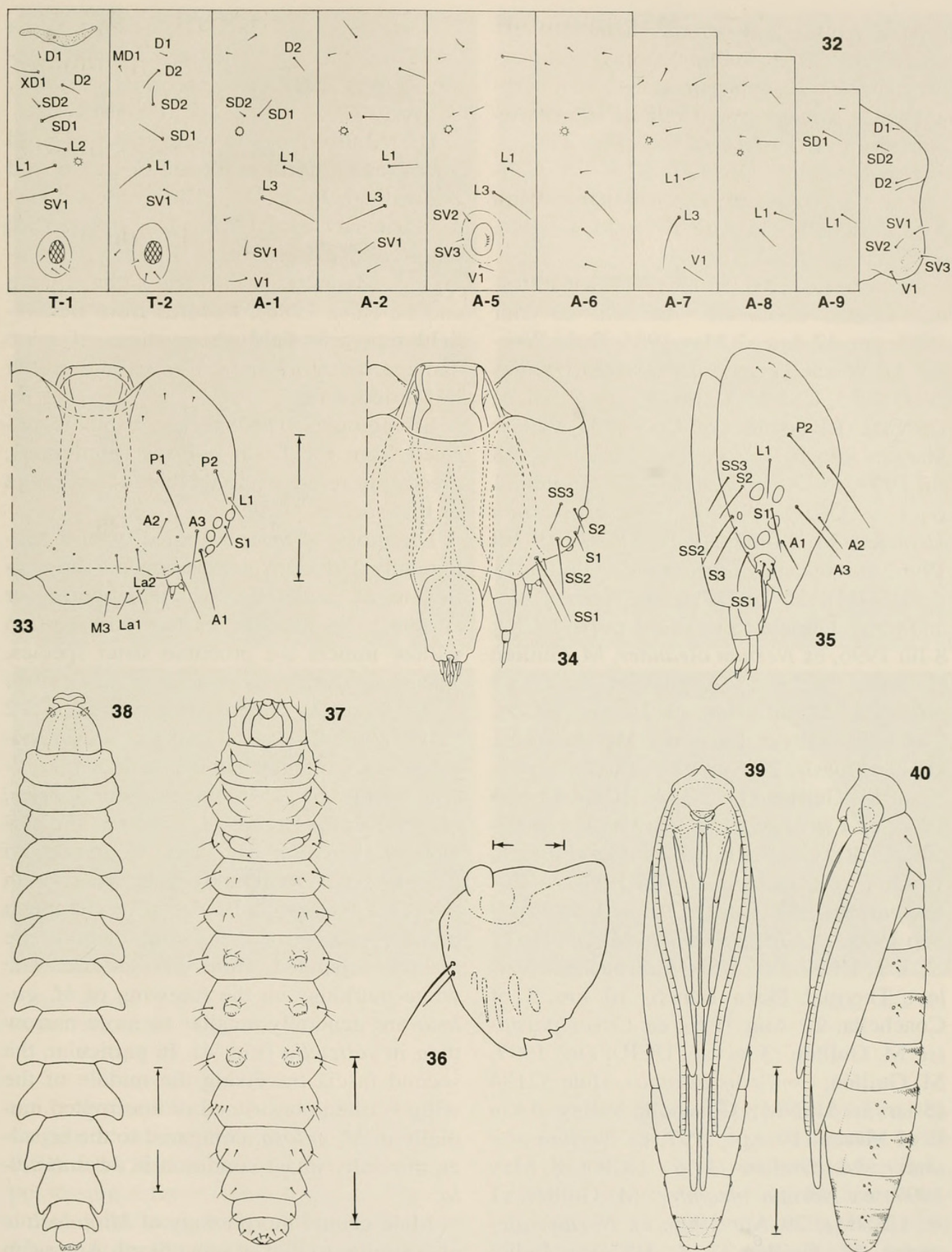
Figs. 32–40. *Marmara gulosa* from grapefruit, morphology of larva and pupa. 32, Spinning larva, chaetotaxy of pro- and mesothorax, abdominal segments 1, 2, 5, 6–10. 33, Head, dorsal view (0.2 mm). 34, Head, ventral view. 35, Head, lateral view. 36, Mandible (0.2 mm). 37, Spinning larva, ventral view (1 mm). 38, Sapfeeding larva, ventral view (1 mm). 39, Pupa, ventral view (1 mm). 40, Lateral view. (Scale length in parentheses.)

ground among leaf litter; ornamented externally by 20–40 minute, frothy, compartmentalized balls approximately 1 mm in diameter; a sinuate row of minute spines meandering over surface of ball (Fig. 31).

Holotype.—♂; UNITED STATES: California: Riverside Co:, Oasis Ranch, 14 km S of Coachella, 26 Aug 1998, M. Guillén, ex *Citrus paradisi.* (USNM).

Paratypes.—UNITED STATES: California: Contra Costa Co: Antioch: 15 Mar 1985, em. 17 Apr–2 May 1985, D. L. Wagner, DLW 85C17, ex *Salix lasiolepis,* slides DRD 4085, USNM 32196 (1 ♂, 4 ♀, DLW, USNM). Riverside Co: Coachella Valley: Shogun Ranch, 16 km S of Coachella: 18 Jul 1997, ex *Citrus paradisi,* M. Guillén (1 ♂, 1 ♀, UCR); 29 Apr 1996, ex *Nerium oleander,* M. Guillén (2 ♂, UCR); 18 Jul 1996, ex *Nerium oleander,* M. Guillén (1 ♂, USNM); 25 Jul 1996, ex *Nerium oleander,* M. Guillén (8 larvae, 1 pupa, UCR); 8 Jul 1996, ex *Nerium oleander,* M. Guillén (1 pupa, UCR); 25 Aug 1998, ex *Citrus paradisi,* M. Guillén (3 larvae UCR). Coachella Valley: Tierra del Mar Ranch, 1 km N of Oasis: 29 Apr 1997, ex *Citrus paradisi,* M. Guillén (1 ♂, 3 ♀, UCR); 11 Sep 1996, ex *Citrus paradisi,* M. Guillén (6 pupae, UCR). Coachella Valley: Oasis Ranch, 14 km S of Coachella: 26 Jul 1998, ex *Citrus paradisi,* M. Guillén (2 ♀, USNM); 9 Sep 1998, ex *Citrus paradisi,* M. Guillén (1 ♂, 1 ♀, UCR, 2 ♂, USNM). Coachella Valley: Thermal Plaza Ranch, 10 km S of Coachella: 20 Aug 1996, ex *Citrus paradisi,* M. Guillén (3 larvae, UCR); Dec 1997, M. Guillén, ex *Citrus paradisi,* slide 32194 (5 larvae, USNM). Coachella Valley: 5 km E of Mecca: 10 Apr 1997, ex *Nerium oleander,* M. Guillén (1 ♂, UCR); 8 May 1997, ex *Nerium oleander,* M. Guillén (1 ♀, USNM); 29 Apr 1996, ex *Nerium oleander,* M. Guillén (1 ♂, USNM). Indio: Oct–Nov, 1960, L. Atkins, ex *Citrus paradisi,* slides USNM 32191, 32192, (1 ♂, 1 ♀, USNM); 14 Mar 1971, L. Atkins, ex *Citrus paradisi,* (1 ♀, USNM). Orange Co: Irvine:, 18 Oct 1997, ex *Persea americana,*

J. Barcinas (1 ♂, USNM). Arizona: Yuma Co.: Yuma: Yuma Valley Agricultural Center: 19 Aug 1997, ex *Gossypium hirsutum,* D. Kerns (2 ♂, UCR; 2 ♀, USNM).

Distribution.—Southwestern United States (as far north as Contra Costa Co. and Bakersfield, Kern Co., California, and east to Maricopa Co. and Yuma Co. in Arizona); reported also from Texas, Florida (Browning, M. Manners, in litt.) and Cuba (Chong and La Rosa 1986). Records from Bakersfield represent field observations of mine damage on citrus and on citrus and cotton in Maricopa Co.

Etymology.—The specific name is derived from the Latin *gulosus* (gluttonous, greedy) in reference to the broad host range of this species.

Diagnosis.—Morphologically and biologically *Marmara gulosa* appears most allied to *M. salictella,* which supports our current belief that the eastern and western willow miners are probable sister species. The basic forewing pattern of *M. gulosa* (Fig. 3)—dark gray to fuscous with 1–2 basal fascia, 2–3 costal and 1–2 dorsal strigulae—is generally similar to that of several North American species. Four species, *M. fraxinixola* Braun, *M. corticola* Fitzgerald, *M. elotella* Ely and *M. fulgidella* (Clem.) have dominantly pale wings with the black background reduced by the much broader pale striae, allowing them to be readily separated from *M. gulosa.* The white markings on the forewing of *M. gulosa* are generally smaller or more narrow than in *salictella* (Fig. 4). In particular, the second fascia traversing the middle of the wing is often constricted or interrupted medially in *M. gulosa,* compared to the broader, normally intact condition in *M. salictella.*

Male genital morphology of *M. gulosa* is also similar to that of most North American species in possessing a deeply divided, trilobed valva (Fig. 5). Within this group the smaller, costal lobe of the valva bears a row of stout spines; the mediolateral cucullar lobe is slender and spatulate; and the ven-
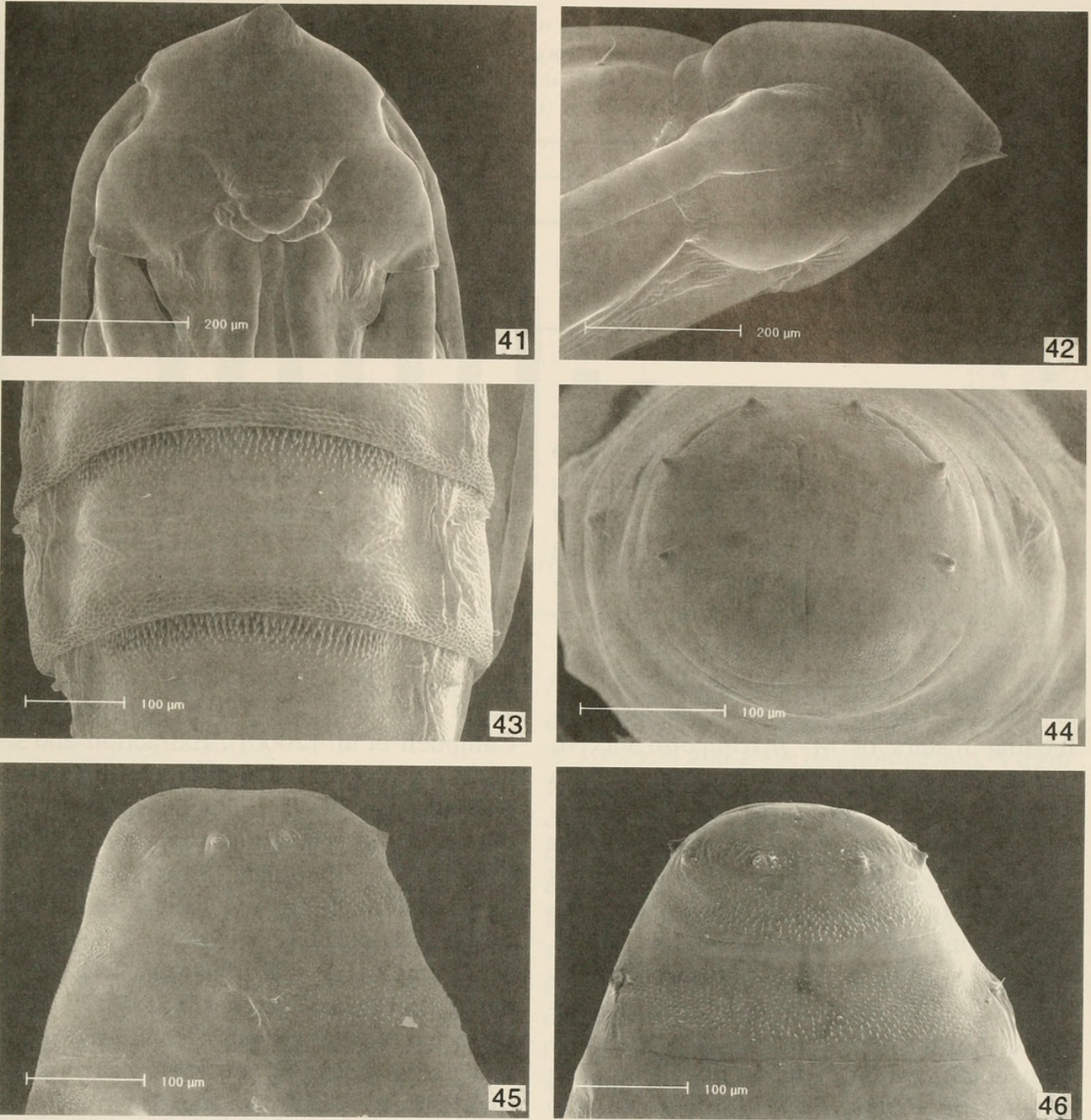
Figs. 41–46. *Marmara gulosa* from grapefruit, pupa. 41, Head, ventral view. 42, Head, lateral view. 43, Dorsal view of A4. 44, Caudal view of A10. 45, Lateral view of A9–10. 46, Dorsal view of A9–10.

tral, valvular lobe is the broadest and most diagnostic in form. The valvae of *M. gulosa* differ from that of *M. salictella* (Fig. 9) in possessing a more reduced apex of the cucullar lobe, and from virtually all other *Marmara* by the expanded subapical costal margin of the valvular lobe (Fig. 5).

The female genitalia of *M. gulosa* and *salictella* are similar in possessing a shallow median cleft in the caudal margin of sternum 8 as well by the greatly reduced, abruptly

flared ostium bursae (Figs. 12–13). The sternal cleft in *salictella* is approximately twice that of *gulosa*. *Marmara pomonella* Bsk., currently represented only by the female holotype from Oregon but also reported from California (Essig 1926), superficially resembles *gulosa* in wing pattern. The female genitalia of *M. pomonella* differ in sternum 8 being deeply excavated, with the ostium bursae heavily sclerotized and more than 3× the diameter of that of *gulosa*.

Table 1. Genetic differences between populations of *Marmara gulosa* on oleander (OL; n = 2), grapefruit (GR; n = 2) and an undescribed species on tree tobacco (TT; n = 1) based on pairwise comparisons of ITS2 (513–557 shared bp) and 28S-D2 rDNA (602–608 shared bp) sequences. Multiple clones sequenced for *M. gulosa* are included in the total number of sequences (t) compared below.

	t	ITS2		28S-D2	
		Bases Differing	Percent Difference	Bases Differing	Percent Difference
within OL/GR	6	0–2	0–0.4	0–2	0–0.3
between OL/GR	6	0–2	0–0.4	0–2	0–0.3
between OL-GR/TT	7	46–47	9.0–9.2	41–42	6.8–7.0

Few larval characters were useful for distinguishing known species. The mandibles in the last sapfeeding instar of *M. gulosa* have three cusps dorsally. The innermost cusp has a series of minute serrations along the outer margin, and the lateral cusp is minutely serrated along both the outer and inner margins (Fig. 16). The inner cusp is serrated in *M. arbutisella*, but the lateral cusp is smooth. The mandibles of the last sapfeeding instars of *M. fraxinicola* and *M. basidendroca* are entirely smooth. In both *M. gulosa* and *arbutisella* the epipharyngeal spines extend across the entire anterior margin of the labrum (Fig. 16); these spines are present only along the basal half of the anterior margin of each labral lobe in *M. fraxinicola* and *M. basidendroca* (Fitzgerald 1973). The labrum in the spinning larvae of *M. gulosa* and *arbutisella* has a median notch, which is reportedly lacking in *M. elotella* (Vinal 1917). Prolegs are also reputedly absent in *elotella*, but this needs further confirmation.

Pupal descriptions are available for only two other species in this genus. *Marmara gulosa* has a single pair of dorsal abdominal setae (D1) and two pairs of shorter setae (SD1,2) located near the spiracles, in segments one through eight (Fig. 40). *Marmara fraxinicola* supposedly lacks SD1 and 2, and *M. elotella* has retained only SD1 and 2.

GENETIC DIFFERENCES

Because of the extreme differences in host plant choice within *M. gulosa*, an ad-ditonal test of population structure was made by comparing sequences of two nuclear genes demonstrated to exhibit differences at the species level: the non-coding interspacer region (ITS2; Forward primer: 5′ TCT AAg Cgg Tgg ATC ACT Cg 3′, Reverse primer: 5′ TAT gCT TAA ATT CAg ggg gT 3′ [reverse primer from Campbell et al. 1993]) and the D2 variable transcript region of 28S rDNA (primers from Campbell et al. [2000]). Extraction and sequencing protocols are outlined in Babcock and Heraty (2000). Sequences were obtained from fresh frozen adults reared from oleander (2 individuals: Shogun Ranch, 10 km S of Coachella, 9 Oct 1997 and 23 Oct 1997), grapefruit (2 individuals: Tierra del Mar Ranch, 1 km N of Oasis, 9 Oct 1997 and Laboratory Colony, Oct 1997 [adults collected from various localities in the Coachella Valley]), and tree tobacco (1 individual: Riverside, 9 Sep 1996). Specimens from willow were not available. Multiple clones were sequenced for some of the individuals for a total of six clones for each of the oleander and grapefruit samples. Sequences are deposited in GENBANK under accession numbers AF280424–AF280430 (285) and AF284564–AF284570 (ITS2).

Few differences were found for either gene between *M. gulosa* reared from grapefruit or oleander (0–0.4%). By contrast, *M. gulosa* and the easily recognized different species from tree tobacco (6.8–9.2%) differed considerably (Table 1). Some variation was observed within the populations, but this was not consistent nor enough to
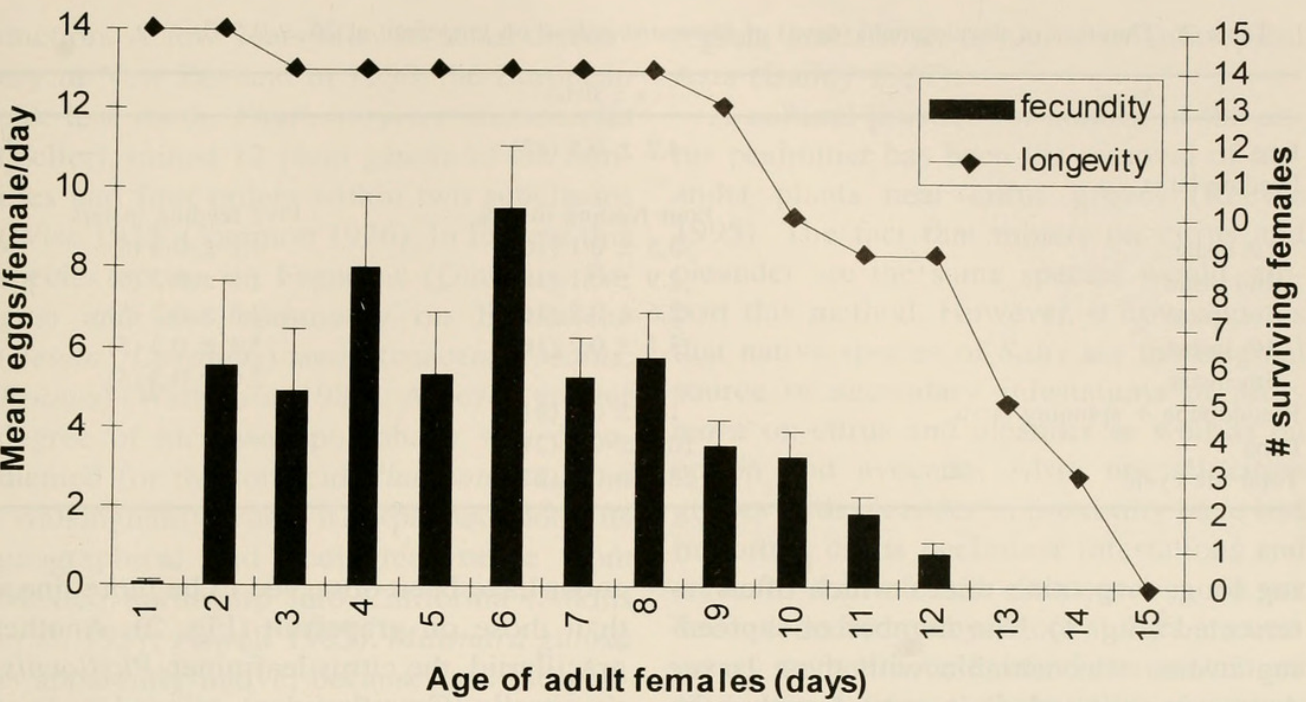
Fig. 47. Age-specific fecundity and survival of *Marmara gulosa* females from grapefruit.

suggest any divergence between populations at this level of analysis.

BIOLOGY

Rearing methods.—Grapefruits with live peelminer larvae were collected in the Coachella Valley, and adults emerged in the laboratory. A colony was started and maintained on grapefruit at room temperature and under natural light. Field-collected fruits were placed in small clear-plastic containers (49.5 × 20.3 × 22.2 cm), and the bottom of each cage was covered with paper towel as a pupation site. Cocoons were cut from the paper towel and placed in small glass vials (15 × 45 mm) closed with a piece of cotton and then placed in a humidified 750 ml clear-plastic container. Relative humidity was maintained at 75% by use of a saturated NaCl solution (Winston and Bates 1960). Newly-emerged adults were released daily into a cage (74 × 46 × 46 cm with wooden walls, the floor and top covered with glass, and the back wall with fine fabric mesh) with grapefruits for oviposition. Food was provided via cotton wool dipped into a 35 ml plastic vial of 10% sucrose solution.

Biological studies.—Studies were carried out in constant temperature cabinets (Percival Scientific Inc., IA) at 26 ± 0.5°C, 75 ± 10% RH and a 14:10 photoperiod. Virgin females and males were paired in individual cages with Rio Red grapefruits. The number of eggs/female/day and longevity of adults were measured. Egg incubation time, larval development, and duration of pupal stage were recorded. The number and duration of each larval instar was recorded by marking the position of the larvae every day and identifying molting periods by larval inactivity.

Eggs were deposited singly on the surface of the fruit. Total fecundity per female was 48.5 ± 7.2 (n = 15) with an average of 4.5 ± 0.8 eggs laid per female per day. Oviposition started 2.9 ± 0.1 days after release of adults in the cages and lasted an average of 7.8 ± 0.7 days with a decline observed after day eight. Little female mortality was observed until day nine (Fig. 47). Adult females survived an average of 10.9 ± 0.8 days (n = 15) and males lived an average of 9.3 ± 1.4 days (n = 14). Eggs hatched after 4.2 ± 0.1 days. Larvae left the eggs by boring directly through the lower surface of the egg into the epidermis of the fruit. Larvae fed in the epidermis, form-

Table 2. Duration of development (days) of *Marmara gulosa* on grapefruit at 26 ± 0.5°C.

Stage	x ± SE (n)	
Egg	4.2 ± 0.1 (42)	
Feeding larva		
	Four feeding instars	Five feeding instars
1st instar	3.5 ± 0.1 (16)	4.2 ± 0.4 (5)
2nd instar	2.9 ± 0.1 (16)	2.2 ± 0.2 (5)
3rd instar	2.6 ± 0.2 (16)	2.8 ± 0.2 (5)
4th instar	3.1 ± 0.2 (16)	3.4 ± 0.2 (5)
5th instar		2.0 ± 0.3 (5)
Pseudopupa + spinning larva	1.0 ± 0.0 (21)	
Pupa	10.6 ± 0.1 (21)	
Total life cycle	28.8 ± 0.4 (21)	

ing long, serpentine mines which often intersected (Fig. 1). The number of sapfeeding instars was variable with most larvae developing through four and a few through five (Table 2), and with males and females present in both groups. After feeding, the final sapfeeding instar became quiescent as the penultimate, nonfeeding transitional instar formed without shedding the cuticle of the former. Appearance of the final, nonfeeding spinning instar thus resulted in shedding of both the last sapfeeding cuticle and that of the transitional instar. The last instar spinning larva then exited the mine, lowered itself from the fruit by a silken thread, and pupated in a slender cocoon in the paper towel provided. The outside of the cocoon was ornamented with small, white, frothy balls. These balls were first discharged from the anus of the spinning larva. Using its mouthparts and legs, the larva then placed the balls on the outside of the cocoon through previously cut slits (as described by Wagner et al. 2000). The slits were then covered with additional silk, and the larva changed to the prepupal stage. The whole larval period lasted 14.1 ± 0.4 days. Adults emerged 10.6 ± 0.1 days after pupation. The entire life cycle required 28.8 ± 0.4 days (Table 2).

The general life cycle is probably the same on oleander, cotton and avocado, as it is in grapefruit, although developmental times will probably be affected by the host plant. Additionally, mines on stems of ole-

ander have been observed to be more linear than those on grapefruit (Fig. 2). Another gracillariid, the citrus leafminer, *Phyllocnistis citrella* (Gracillariidae), mines leaves of *Citrus* spp., although it will occasionally mine the fruit epidermis (Heppner 1995). *Marmara gulosa* will also occasionally mine shoots of citrus (Atkins 1971, Gibson et al. 1997). The citrus leafminer occurs on citrus in most regions of the world (Heppner 1993, 1995; Garrido 1995), including California. The main difference between mines by *M. gulosa* and *P. citrella* is in the deposition of frass, with that of *P. citrella* forming a slender, brownish black trail down the middle of the mine; a distinct frass trail is not present in *M. gulosa*. Both species form a serpentine mine, but that of *M. gulosa* consists of a wandering, more convoluted gallery that often intersects (Fig. 1). The mine of *P. citrella* tends to be more compact and does not intersect.

Discussion.—*Marmara gulosa* may be one of the most polyphagous species of Gracillariidae. Most species of Gracillariidae are either monophagous or oligophagous, usually restricting their feeding to a single plant family. More general feeders include two species of the southeastern Asian genus *Conopomorpha*, which mine as many as five plant genera belonging to three families in as many orders (Bradley 1986). As has been observed with other introduced insects, a few Gracillariidae have expanded their host range following intro-

duction. A few years after its intial discovery in New Zealand in 1950, the European oak leaf moth, *Phyllonorycter messaniella* (Zeller), mined 12 plant genera of six families and four orders within two subclasses (Wise 1953, Common 1976). In Europe this species occurs on Fagaceae (*Quercus, Fagus*) and less commonly on Betulaceae (*Betula, Carpinus*) and Rosaceae (*Malus, Prunus*) (Watkinson 1985). An even greater degree of increased polyphagy was documented for the tortricid *Platynota stultana* (Walsingham) when it expanded both its geographical and ecological range from Mexico northward into California (Atkins et al. 1957, Powell 1983). *Marmara gulosa* is apparently native, because it is morphologically similar to other indigenous *Marmara* and feeds on native *Salix*.

Within *Marmara,* species are usually host plant specific or even specific to a particular structure on the same host plant (Fitzgerald 1973, Davis and Feller, unpublished). Of those species occurring in North America, each species feeds on a single host species, or if present on more than one, the plants at least belong to the same genus or family. Additionally, when a *Marmara* species occurs on more than one species of host plant, usually the same structure of the plant is attacked (Table 3). *Marmara gulosa* is unusual in being broadly polyphagous, with verified rearing records from five families in four of the six recognized subclasses of dicotyledonous plants (Heywood 1993) (Table 4), including *Citrus* (grapefruit, etc.), *Gossypium* (cotton), *Nerium* (oleander), *Persea* (avocado), and *Salix* (willow). Moreover, larvae of this species have been observed to mine different structures of their hosts; e.g., fruit peel and shoots of citrus, shoots and leaves of oleander, stems of cotton, fruits and shoots of avocado, and shoots of willow. Notably, except for *Salix lasiolepis,* none of these species is native to California. *Persea americana* and *G. hirsutum* are probably neotropical in origin; *Nerium oleander* is from the Mediterranean region, and *Citrus* is native to subtropical Asia (Bailey 1957).

A cultural practice for control of the citrus peelminer has been the removal of oleander plants near citrus groves (Reeves 1995). The fact that miners on citrus and oleander are the same species would support this method. However, it now appears that native species of *Salix* are the original source of secondary infestations of *Marmara* on citrus and oleander as well as on cotton and avocado. Also, not all citrus groves with oleander in proximity have had important citrus peelminer infestations and some of the infested citrus groves do not have oleander nearby. More studies are necessary to better understand the movement of the moth from *Salix* to other secondary plant hosts.

In Arizona, the citrus peelminer mines stems of cotton during the summer, presumably without causing important damage to the plants (D. Kerns, personal communication). Cotton is harvested in these areas in September when increasing populations of peelminer on citrus have been reported (Gibson et al. 1997). The deterioration in quality of cotton as it senesces may lead to a shift by emerging adults to citrus. This may also be the case with oleander, on which larvae mine only fresh new shoots. A shift to citrus may correlate with the absence of fresh growth in the early summer.

Table 3. Host and tissue specificity of *Marmara* species.

Marmara Species	Host Plant	Family	Part Mined	References
colspan_header	Three species share one host species			
M. basidendroca Fitzgerald	*Fraxinus pennsylvanica* Marsh.	Oleaceae	Stem: base of tree, root collar	Fitzgerald 1971
M. corticola Fitzgerald	*Fraxinus pennsylvanica* Marsh.	Oleaceae	Stem: branches (periderm and cortex)	Fitzgerald 1971
M. fraxinicola Fitzgerald	*Fraxinus pennsylvanica* Marsh.	Oleaceae	Stem: branches (periderm)	Fitzgerald 1971
colspan_header2	Species reported from a single plant genus/species			
M. elotella Busck	*Malus* sp.	Rosaceae	Twigs	Vinal 1917
M. fasciella Chambers	*Pinus strobus* Ehrh.	Pinaceae	Stems	DeGryse 1943
M. isortha Meyrick	*Theobroma cacao* L.	Sterculaceae	Pods	Bondar 1939, Meyrick 1915
M. opuntiella Busck	*Opuntia* sp.	Cactaceae	Leaves	Busck 1906, Forbes 1923
M. pomonella Busck	*Malus* sp.	Rosaceae	Fruit	Clemens 1860
M. salictella Clemens	*Salix vitellina* L.	Salicaceae	Bark	Clemens 1863
M. serotinella Busck	*Prunus serotina* L.	Amygdalaceae	Stems	Forbes 1923
colspan_header3	Species reported from two plant genera within same family			
M. arbutiella Busck	*Arbutus* sp.	Ericaceae	Leaves	Vinal 1917
	Arbutus menziesii Pursh.	Ericaceae	Leaves	Wagner et al. 2000
	Arctostaphylos andersonii Gray	Ericaceae	Leaves	Wagner et al. 2000
M. auratella Braun	*Rudbeckia lacinata* L.	Asteraceae	Stems	Forbes 1923
	Dahlia sp.	Asteraceae	Stems	Forbes 1923
M. fulgidella Clemens	*Quercus* sp.	Fagaceae	Twigs	Clemens 1860
	Castanea sp.	Fagaceae	Twigs	Clemens 1860
M. smilacisella Chambers	*Smilax glabra* Roxb.	Liliaceae	Leaves	Chambers 1875
	Smilax hispida Muhl. ex Torr.	Liliaceae	Leaves	Braun 1923
M. oregonensis Fitzgerald	*Pseudotsuga menziesii* (Mirb.) Franco	Pinaceae	Bark	Fitzgerald 1975
	Abies grandis (Dougl. ex D. Don) Lindl.	Pinaceae	Bark	Fitzgerald 1975

Table 4. Classification of Plant Hosts of *Marmara gulosa.*

Subclass	Order	Family	Genus
Magnoliidae	Laurales	Lauraceae	*Persea*
Dilleniidae	Malvales	Malvaceae	*Gossypium*
Dilleniidae	Salicales	Salicaceae	*Salix*
Rosidae	Sapindales	Rutaceae	*Citrus*
Asteridae	Gentianales	Apocynaceae	*Nerium*

side CA); Michael Maurer (University of Arizona); Harold Browning (Citrus Research and Education Center, Lake Alfred FL); Jaroslaw Buszko (Uniwersytet Mikolaja Kopernika, Torun, Poland); Don Frack (Los Angeles Co. Agricultural Commissioner Office, El Monte CA); Tosio Kumata (Ebutu City, Hokkaido, Japan); Malcolm Manners (Florida Southern College, Lakeland); Orlando Aponte (UCR); David Headrick (University of California, San Luis Obispo); Rosser Garrison (Los Angeles Co. Agricultural Commissioner Office, El Monte CA); Craig Kallsen (University of California, Cooperative Extension, Bakersfield) and Eric Natwick (University of California Desert Research Extension, Holtville, CA) provided valuable information. Vichai Malikul and Young Sohn (Smithsonian Institution, Washington, DC) are responsible for figs. 3–13 and 32–40 respectively.

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